STRUCTURE AND DIVERSITY OF A RIPARIAN FOREST AT KAIETEUR NATIONAL PARK, GUYANA

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ABSTRACT

Kaieteur National Park, encompassing middle portions of the Potaro River, Guyana, contains a mosaic of habitats from exposed sandstone to riparian forests (100 – 450 m) with soils of the riparian forests of course white sand with very little peat. As part of an ecological study, two one-hectare plots were established in the Wallaba (*Eperua*)–mixed forest of the Potaro Plateau to document the species diversity and tree composition within the park. Approximately 133 species in 33 families comprised 1585 trees with a DBH ≥ 10 cm. *Chamaecrista adiantifolia* var. *pteridophylla* and *Eperua falcata* (Leguminosae-Caesalpinioideae) accounted for 26.1% of all trees inventoried in the plots. Of the three subfamilies of Leguminosae, Caesalpinioideae had over 300 stems/ha at Kaieteur. We used two 1 ha plots at each site to compare the forest at Kaieteur with the lowland forest of Kwakwani (Guyana) and Barro Colorado Island (Panama). Of these three, Kaieteur had the highest number of stems (69.6%) < 20 cm DBH and highest total basal area (66 m^2 / ha). Statistical analysis of the two plots at Kaieteur clearly indicates a high degree of floristic differences between the Kaieteur sites in this Wallaba (*Eperua*)–mixed forest. Although dominated by *E. falcata* and *C. adiantifolia* var. *pteridophylla*, the plots at Kaieteur indicate there are differences in the forest community over a very short distance. This may be attributable to subtle changes in microhabitats and/or species dynamics of the subdominant tree taxa of the Potaro Plateau.

Key Words: Barro Colorado Island, Guiana Shield, Kwakwani, Pakaraima Mountains, plots, Roraima sandstone

RESUMEN

El Parque Nacional de Kaieteur localizado a lo largo del curso medio del río Potaro en Guyana, es un mosaico de hábitats que incluye desde areniscas expuestas hasta bosques ribereños (100–450 m) con suelos de arenas blancas con muy bajos contenidos de materia orgánica. Como parte de un estudio ecológico, se instalaron dos parcelas de 1 ha en el Wallaba (*Eperua*)-bosque mixto del altiplano de Potaro - a los efectos de documentar la diversidad especifica y la composición del dosel arbóreo dentro del Parque. En ambas parcelas se encontraron un total de 1585 individuos con DAP mayor a 10 cm, los que se correspondieron con aproximadamente 133 especies reunidas en 33 familias. *Chamaecrista adiantifolia* var. *pteridophylla* y *Eperua falcata* (Leguminosae-Caesalpinoideae) constituyeron el 26.1% del total de los tallos inventariados. De las tres subfamilias de Leguminosas, Caesalpinoideae fue la mejor representada en las parcelas de Kaieteur, con mas de 300 tallos/ha. Utilizamos parcelas de 1 ha para comparar el bosque de Kaieteur con los bosques de tierras bajas ubicados en Kwakwani (Guyana) y en la Isla de Barro Colorado (Panamá). De los tres bosques comparados, Kaieteur tuvo el mayor numero de tallos (69.6%) con DAP menores a los 20 cm, y la mayor área basal total (66 m^2/ha). El análisis estadístico de las dos parcelas en Kaieteur indican claramente que existen grandes diferencias florísticas entres ellas. Auque ambas parcelas son dominadas por *E. falcata* y *C. adiantifolia* var. *pteridophylla*, estas muestran diferencias en la composición y estructura a lo largo de cortas distancias. Estas diferencias pueden deberse a cambios sutiles de microhábitat y/o a las diferentes interacciones entre las especies de árboles sub-dominantes del altiplano de Potaro.

INTRODUCTION

Kaieteur National Park (Fig. 1), the only national park in Guyana, is located approximately 230 km southwest (5° 10' 42" N; 59° 29' 44" W) of Georgetown, the nation's capital. The park is situated on an upland region of Guyana known as the Potaro Plateau of the Pakaraima Mountains. This plateau is an eastern extension of the largely Venezuelan Roraima sandstone formation that forms the flat table-top mountains known as tepuis. The Potaro River flowing over this plateau has cut a 20 km gorge in the easternmost portion of the Roraima formation. The river eventually plunges 226 meters via a single drop into the gorge. Kaieteur Falls is one of the most spectacular cataracts in the world and is the main geological feature of the national

park. The park was established in 1929 and encompassed 44 km^2 to protect the area around the falls, the Potaro gorge, and the surrounding Potaro Plateau. Today the park has been expanded to 627 km^2 to protect a greater representation of the vegetation around the falls and a larger expanse of the savannas and forests of the plateau. In 1998, the park was incorporated into the National Protected Areas System (NPAS) that is currently being developed as part of Guyana's ecotourism business. With this NPAS Project, Guyana urgently needs information on the biodiversity of the area before any conservation or management policy can be implemented. Botanical exploration of the mid- to lower portions of the drainage has been limited to the area around the falls and along the Potaro gorge; such exploration has resulted in a checklist of the vascular plants of the area (Kelloff & Funk 1998), but there have been virtually no ecological studies in an attempt to quantify species diversity.

In general, tropical forests have been characterized as having a high diversity of trees, with some inventories recording over 300 species with a diameter at breast height (DBH) ≥ 10 cm per hectare (Gentry 1988; Hubbell & Foster 1986; Valencia et al. 1994). Several hypotheses offer explanations regarding the maintenance of high diversity. Huston's (1979, 1994) "dynamic equilibrium hypothesis" suggests that diversity in populations is reached by low rate of competitive displacements or by periodic reductions in species (Huston 1979). If the population has a high number or high frequency of disturbances, slow-growing species will disappear and be replaced by the faster-growing pioneer species over time thus reducing diversity. In order to overcome this species must have some minimum growth rate to recover from population reductions. In other words, an increase in growth rates during periods of high frequencies of population reduction can actually increase diversity (Huston 1979). Another hypothesis is an ecological response to environmental conditions such as low and high light conditions. By changing the availability of resources, disturbances such as canopy gaps may influence succession. Those species efficient in recruitment quickly move in, and the site becomes covered with pioneer species (Bazzaz & Picket 1979). The ability to survive under low light conditions and the ability to achieve high growth under high light conditions is the most significant difference between species diversity (Bazzaz & Picket 1979; Hubbell 1995). It's the survival of the fittest that can utilize the disturbance, increasing the diversity of species. In Guyana, *Dicymbe* Spruce ex Benth., which is locally known as clump wallaba, produces coppices (suckers) on the healthy parent tree. When the parent trees die, these young trees can take advantage of the mature root system of the parent, as well as the light gap, and thus can out-compete other species in the area (Henkel 2003; ter Steege et al. 1993).

Not all tropical forests show a high alpha tree diversity, however. Productivity and disturbance vary in the tropics (Richards 1952; Connell & Lowman 1989), and this is evident in the mixed forests of central Guyana where there is a tendency for some species to dominate the vegetation (Davis & Richards 1934; Fanshawe 1952; Johnston & Gillman 1995; ter Steege 1993). Several examples of this type of forest in Guyana are the wallaba (*Eperua* Aubl.), mora (*Mora* Benth.), or clump wallaba (*Dicymbe*) forests (Davis & Richards 1934; Fanshawe 1954; Henkel 2003; ter Steege 2000b). These forests have a few species that represent a high percentage of the stems and/or basal area.

The tropical forest of Guyana contains a wide array of forest types, e.g., mangrove, moist and dry evergreen, montane, seasonal, swamp, and Greenheart forests. In swamp and mangrove forests, edaphic factors such as flooding and soil clearly explain these forest types (Fanshawe 1952). However, in the mixed forests of Guyana, the relationship between soil, hydrology, and forest types is not clear (ter Steege et al. 1993). Generally, classification of forest types has largely been based on climate, soil, and physiognomy (Ducke & Black 1954; Prance 1987), which reference species compositions or have generalized tropical floras at the genus or family level (Forero & Gentry 1988; Maguire 1970; ter Steege et al. 2000a). Recent studies used plots to examine patterns of plant diversity, e.g., how species richness (Gentry 1988) or habitat diversity contributes to species diversity (ter Steege 1993; Sabatier et al. 1997; Tuomisto & Ruokolainen 1997). Plot studies produce data at the species level and can provide long-term information on growth, mortality, regeneration, and dynamics of forest trees.

Sampling riparian trees of the plateau using a grid system of collecting allows us to (1) describe the



Fig. 1. Kaieteur Falls, located along the Potaro River in Guyana, has a single drop of 226 m into the splash basin below.

relative abundance and distribution of the trees, (2) provide a framework by which the forest structure of Kaieteur can be compared to other known study sites, (3) help fill in the missing tree taxa in the checklist, and (4) provide a standard by which forest structure and composition can be measured.

This paper presents the results of the two, one-hectare (ha) inventories carried out on the Potaro Plateau within Kaieteur National Park. Tree data from two other plot studies were used as a comparison of the tree diversity at Kaieteur. Data from two one ha plots were borrowed from a lowland forest in Guyana near the town of Kwakwani (a Guiana Shield community) and two one ha portions of a 50 ha plot at Barro Colorado Island, Panama (non-Guiana Shield community). In general, plot data from the Guiana Shield and particularly the Potaro Plateau are scarce (ter Steege et al. 2000a). One ha plots allow for us to quantify the relationship between tree species as well as among tree species and add to the knowledge of the tree diversity of Potaro Plateau in Guyana. The ultimate goal of this project was to document the species diversity and tree composition of the Wallaba (*Eperua*)-mixed forests of the Potaro Plateau and to compare the tree species diversity of Kaieteur National Park to those of other plots.

METHODS

The study site.—Kaieteur National Park is a mosaic of habitats consisting of exposed sandstone, grass savanna, scrub, and riparian forests. The average air temperature for the year is 26.5°C (USDA 1974). The average rainfall for the northeast face of the Pakaraima escarpment is approximately 3750 mm per year (Fanshawe 1953). Two 1 ha plots were established in the Wallaba (*Eperua*)-mixed forest of the Potaro Plateau. The study was conducted between 1995 and 1998 with sites selected based on the surrounding vegetation. In both 1 ha plots, some level of previous human disturbance was found (e.g. several large trees were removed for the building of the guesthouse). The first plot (Fig. 2a) is located at the headwaters of the Korume Creek (5°10'42"N, 59°29'44"W). The lower portion of the first plot is seasonally inundated and includes a portion of the creek in which grew a few patches of *Thurnia sphaerocephala* (Rudge) Hook.f. Along the western side of the plot, the land gradually rises up the ravine towards Muri-Muri savanna. The second plot (Fig. 2b) was established in the upland forest of the plateau between the Korume Creek and Potaro River gorge (5°11'16"N, 59°28'52"W). The terrain is rocky with a slight downward slope towards the northeastern part of the trail. There is no evidence of seasonal flooding as in the first plot.

The soils from these two sites were not analyzed, but it was generally observed that they consisted of a course white sand of quartzite with very little peat. These shallow white sand areas of the Pakaraima Plateau (Fanshawe 1954) are associated with the peneplain of the interior of Guyana.

The plots in the lowland area of Guyana used for comparison are located near the town of Kwakwani at the Aroaima (bauxite) mining site on the Berbice River, 238 km up the Canje River from New Amsterdam (5°30'N, 58°W). Data for these plots were kindly provided by James Comiskey (Smithsonian Institution Man in the BioSphere Program). The average rainfall recorded for this area is 2400 mm per year. The land is low lying with swampy areas near the river. The sites for the plots were selected within the area designated as "south mine," a proposed area for future bauxite mining. In this area, the shallow layer of topsoil (averaging 1.5 meters in depth) covers ca. nine meters of bauxite that overlays 60 meters of volcanic rock. Both plots were irregular in shape, and the vegetation is classified as non-flooded tropical mixed forest (Comiskey et al. 1994). It was noted that the soil was composed of a mixture of sand and clay with high porosity and high drainage. The soils were not sampled (Comiskey et al. 1993).

The second set of plots were part of a 50 ha study site at Barro Colorado Island (BCI) located near the Panama Canal at the Smithsonian Tropical Research Institution's station (9°9'17"N, 79°50'53"W). This forest is classified as a rich, old growth tropical forest dominated by Bombacaceae and Leguminosae (Condit et al. 1996). The terrain on the island's summit is relatively level with a variance of 28 meters in elevation. The average rainfall for this area is about 2500 mm per year (Condit et al. 1996) with a mean annual temperature of 27°C. The soil at BCI is a clay-rich tropical soil with an organic matter content (Yavitt 2000). Data from two of the 50 1 ha plots (designated as Hec21 & Hec37) were selected and kindly provided by Richard Condit for this study.

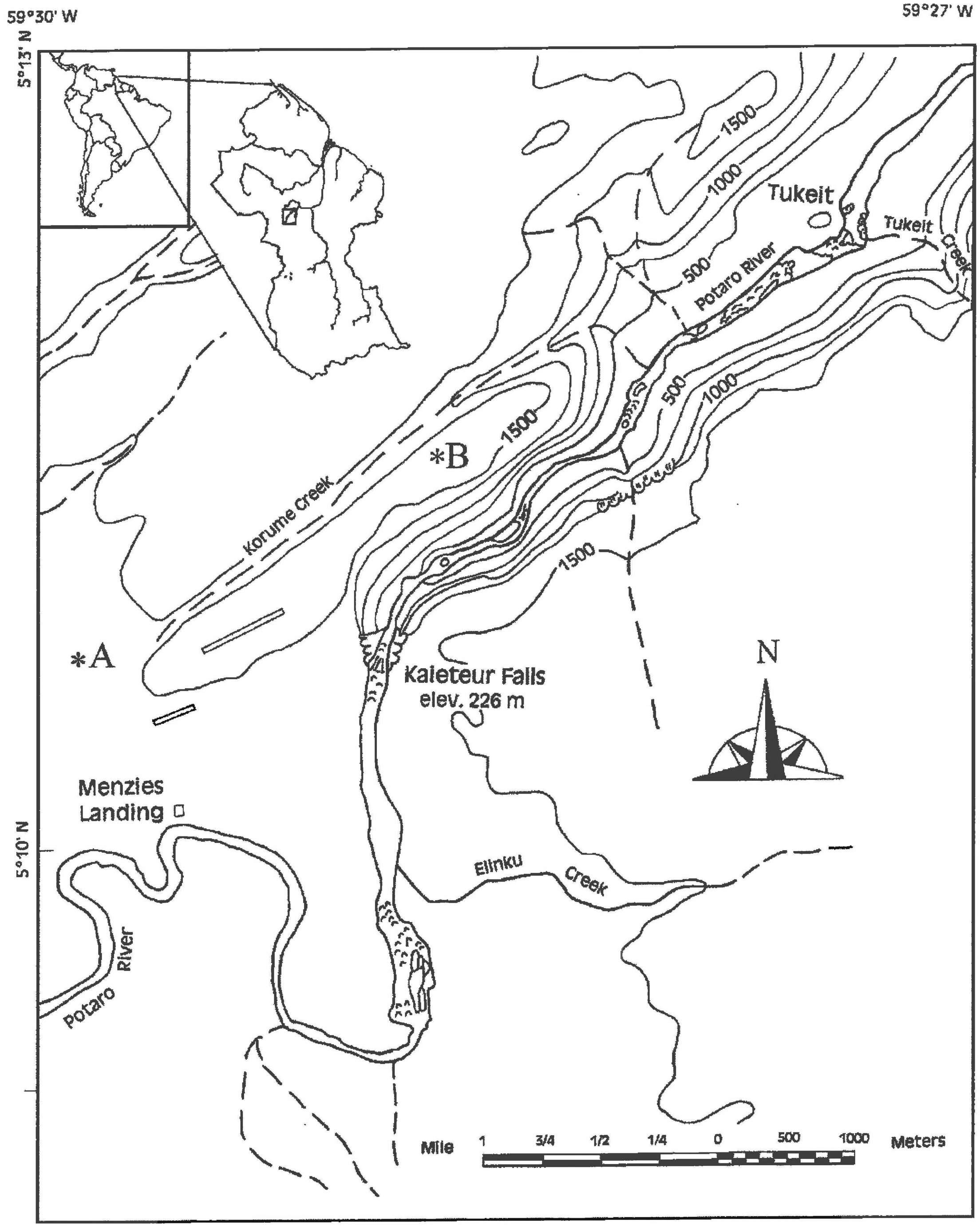


FIG. 2. Kaieteur National Park is located on the eastern portions of the Roraima formation. A. plot KF1 is located at the headwaters of the Korume Creek; B. plot KF2 is located near the Tukeit–Kaieteur trail on the plateau.

Established on the central plateau of BCI, the 50 ha permanent plot has a 70 year history of the flora and fauna and over 1500 scientific papers written on various topics (Hubbell & Foster 1992). For more information on Barro Colorado Island, selected readings are: Hubbell and Foster 1992 and Hubbell et al. 1995.

Census methods.—The method adapted for inventorying the woody vegetation of Kaieteur followed Dallmeier (1992). The terrain at both sites was uneven, and corrections were made to adjust for slope (Durr et al. 1988). The two 1 ha plots at Kaieteur were subdivided into 25 contiguous 20 × 20m quadrats, and all stems with a minimum DBH of 10 cm were measured. Spatial location of the trees within each quadrat was recorded for mapping purposes. Field vouchers were obtained, where possible, for each species encountered. Information was recorded to aid in identifications of the sterile vouchers, e.g.,features of the wood, bark, and sap (Polak 1992; Rosayro 1953). Romeo William, tree spotter and guide, assisted in the identifications of trees in the field. Local or vernacular names for trees (Fanshawe 1947, 1953, 1954) helped to identify morphologically similar trees. Most vouchers were sterile and thus required extensive time in the herbarium for identification. Trees were identified to the species level when possible, but were otherwise assigned to morphospecies.

Taxonomic nomenclature followed the "Checklist of the Plants of the Guianas: Guyana, Surinam, French Guiana" (Boggan et al. 1997). Voucher specimens were deposited in the Guyana National Herbarium, University of Guyana (BRG) and at the U.S. National Herbarium, Washington, DC (US).

Density, frequency, and dominance were calculated to describe how individual species are spatially distributed within the plot and how these distributions contribute to the community (Barbour et al. 1987). **Stem basal area (a)** and density of each tree were calculated using a = 0.7854 × (DBH) 2, where a = basal area of each tree in m^2 (Anderson & Ingram 1989). This measurement is useful in estimating canopy cover of trees because it assumes to take trunk **diameter at breast height (DBH)** into account. We also calculated **species basal area (BA)**, defined as the sum of all stem basal areas (a) of a given species. **Density** is defined as the number of trees per hectare, and **relative density** is the percentage of one species in relation to the total plant diversity. **Relative frequency** is expressed as a percentage of the number of quadrats that contain a given species. Dominance is an important ecological measurement. A species that contributes the most cover or basal area to the community is considered the dominant species. **Dominance** is calculated as the percent of basal area of a given species to total basal area (Balslev et al. 1987).

Finally, the relative contribution that a species provides to the community is called its importance value (Balslev et al. 1987). The **importance value index (IVI)** can be calculated by the addition of the relative density, frequency, and dominance for each species and for all trees at each site. High IVI values indicate that a species has a high basal area, frequency, and density at a site or when one or two of these parameters are much higher than other species (Felfili & da Silva 1993). The sum of relative parameters places species in a hierarchical order in the community and is useful for comparisons between different sites (Curtis & McIntosh 1951; Felfili & da Silva 1993). The IVI values can range from 0 to 300, with 300 representing a pure stand of one species (Balslev et al. 1987).

Statistical analyses.—Spatial and temporal variations in tropical tree communities can complicate the process of describing forest structure (Dutilleul 1993; Hall et al. 1998), and raw species data from plots can be too large and cumbersome to yield any meaningful intrinsic patterns. Ordination can reduce species abundance data into a space with fewer dimensions that can reflect sample configurations in ecological space (Gauch & Whittaker 1981). In community ecology, such ordinations can describe some of the strongest patterns in species composition (McCune & Mefford 1999; McCune & Grace 2002). Ecologists have applied metric ordination, which includes principal components analysis (PCA), to analyze vegetation data (Proctor 1967; Debinski & Brussard 1994; Tuomisto et al. 2003). This type of ordination assumes a linear relationship between the variables and is rarely amenable to ecological community data; it can also lead to considerable obscurity in data interpretations (Goodall 1953). Non-metric ordination methods are considered more powerful for analyzing vegetation data because this method assumes a non-linear relationship between the

variables and the use of ranked distances tends to linearize the relationship between the distances measured in environmental space and species space (McCune & Mefford 1999).

Species data per plot were summarized into data matrices (taxon vs. quadrat) and imported into PC-Ord (McCune & Grace 2002), a multivariant statistical program. Because the data represent quantitative scores per taxon, the original values were log transformed using $b_{ij} = \log(x_{ij} + 1)$, where the value of one is added to each species score to define zero values in the data. Log transformation reduces any dominant effects and normalizes the relative importance of common or rare species (Digby & Kempton 1987; McCune & Grace 2002). To visualize multivariate patterns among the quadrats, non-metric multidimensional scaling (NMS) was conducted using Sørensen (Bray-Curtis) distances for each plot and on each plot pair. NMS in PC-Ord is based on Mather's (1976) program and the algorithm of Kruskal (1964).

For each dataset in this study, the "autopilot" mode in PC-Ord was used. This mode provided a random starting configuration for each run. The program calculates each solution by running 40 runs with the real data and 50 runs with the randomized data, with a maximum number of 400 iterations for six axes. The program selected the best solution at each dimensionality where $p \leq 0.05$ for the Monte Carlo test and where that value of the "stress" parameter was the smallest number. Clarke's (1993) "rules of thumb" were used to interpret the final stress. Clarke found that most ecological community data will have values with a final stress between 10 and 20.

NMS provides an optimal ordination technique to analyze patterns in tree species composition for each of the studies. The final result in each analysis was an ordination in two-dimensional space. The two axes show the relationship between species abundance and the axis score.

RESULTS

Kaieteur National Park, Guyana.—There were 1724 total number of stems ≥10 cm DBH at Kaieteur in the two study plots. These stems covered a total basal area of 66.34 m²/ha. Plot KF1 at Kaieteur contained 757 stems per hectare, with most taxa represented by a single stem. *Dicymbe pharangophila* R.S. Cowan (swamp wallaba, Leguminosae–Caesal.) produced coppice shoots from the base of the trunk that resulted in 65 stems being measured and tagged from a total of 28 trees. This habit of producing multiple stems from the base was also noted by Whitton (1962) and Henkel (2003) of *Dicymbe corymbosa* Spruce ex Bentham, another "swamp wallaba" found on the Potaro Plateau. The largest diameter tree recorded for the site was *Ocotea* sp. (Lauraceae), with a DBH of 89 cm. Other species with a DBH > 60 cm were *Pouteria* cf. *cuspidata* (A. DC.) Baehni (Sapotaceae) and *Swartzia schomburgkii* Bentham (Leguminosae–Fab.). Sixty-four percent of the stems were under 20 cm in diameter, and only one percent of the trees reached over 60 cm DBH. The two species that had the highest Important Value Index (IVI) were *Chamaecrista adiantifolia* (Spruce ex Bentham) H.S. Irwin & Barneby var. *pteridophylla* (Sandwith) H.S. Irwin & Barneby (Caesal.; IVI=20.052) and *Eperua falcata* Aublet, (Caesal.; IVI=15.427). These two species were found throughout the plot and accounted for 13.4% of the stems. *Dicymbe pharangophila* (IVI=14.679), *Ormosia coutinnoi* Ducke (Fab.; IVI=10.109), *Dicymbe* sp. (IVI=10.027) and *Pouteria cuspidata* (IVI=10.442) ranked next in importance. These species accounted for 32% of total stems recorded for KF1.

The understory species were not recorded, but it was noted that two species of Marantaceae (*Ishnosiphon* sp. and *Monotagma spicatum* (Aublet) J.F. Macbride) dominated the lower wet areas of the plot. One species of Bromeliaceae (*Ananas parguazensis* L.A. Canargo & L.B. Smith) dominated the dryer soils of the plot. *Thurnia spherocephala* (Ridge) Hooker f. (Thurniaceae) was quite abundant and grew in the flowing waters of the creek.

The second plot (KF2) at Kaieteur had more stems (967) than the first plot. *Dicymbe pharangophila* was nearly absent from this plot. *Chamaecrista adiantifolia* var. *pteridophylla* (95 cm DBH) and *Swartzia schomburgkii* Bentham (Fab.; 92 cm DBH) were the largest trees recorded for the site, followed by *Elizabetha* sp. (Caesal.; 66 cm DBH) and *Pouteria cuspitata* (64 cm DBH). Stems 20 cm DBH or less accounted for 69.5%, whereas only 1.0% of the stems exceeded 60 cm in diameter. Several species ranked high in IVI: *Eperua*

falcata (IVI=20.048), *Chamaecrista adiantifolia* var. *pteridophylla* (19.486), *Ocotea* spp. (IVI=18.253), and *Swartzia schomburgkii* (IVI=17.404). When *Catostemma commune* Sandw. (Bombaceae; IVI =15.082), *Ormosia coutinnoi* (IVI=12.328), and *Eperua* spp. (IVI=15.702) are added, these species account for 40.3% of the total stems recorded for plot KF2. The understory species were not surveyed, but it was noted that *Ishnosiphon* sp. and *Monotagma spicatum* were somewhat evenly distributed in the plot. *Vriesea splendens* (Brongn.) Lem. (Bromeliaceae) was seen along with the spiny bromeliad (*Ananas parguazensis*) from the first plot but was not as abundant. A broad-leaf aroid grew on tree trunks, and a Rapateaceae (*Stegolepis ferruginea* Baker f.) dominated the understory at quadrat 14.

In both plots at Kaieteur, the Leguminosae had the highest number of individuals per site (815 stems or 47.3% of the plots) most of which were from the subfamily Caesalpiniodeae (607). In plot 1 Bombacaceae ranked as the second most abundant family across all quadrats with 64 stems. Bombaceae, in plot 2, had 77 stems but ranked third after Lauraceae (136 stems).

Kwakwani, Guyana.—There were a total of 995 stems ≥ 10 cm DBH at Kwakwani in the two plots, these with a total basal area of 52.13 m²/ha. Five hundred and seven stems were recorded from first plot (AR1) at Kwakwani. Only four trees had a second stem measuring over 10 cm DBH. The largest tree on the site was *Trymatococcus amazonicus* Poepp. & Endl. (Moraceae) at 91 cm DBH. *Eschweilera pedicellata* (Rich.) S.A. Mori (Lechythidaceae) represented 23% of the total stems (115 stems) in this plot and had an IVI of 33.425. The taxon with the next highest IVI (6.751) was *Aspidosperma excelsum* Benth. (Apocynaceae) followed by *Bocageopsis multiflora* (Mart.) R.E. Fr. (Annonaceae; 6.733), *Unonopsis rufescens* (Baill.) R.E. Fr. (Annonaceae; 6.190), *Swartzia schomburgkii* (Fab.; 5.116), *Prunus* sp. (Rosaceae; 3.857), and finally *Cordia sagotti* I.M. Johnst. (Boraginaceae; 3.795). These taxa represented 163 stems or 21% of the stems counted in the site. Sixty three percent of the stems were under 20 cm DBH and only 2% were over 60 cm DBH: *Eschweilera pedicellata* (Lecythidaceae; 88.2 cm), *Aspidosperma excelsum* (Apocynaceae; 85.9 cm), *Albizia niopoides* (Spruce ex Benth.) Burkart (Leguminosae–Mimos.; 83.5 cm), *Inga pezizifera* Benth. (Mimos.; 76 cm), and *Bocageopsis multiflora* (Mart.) R.E. Fr. (Annonaceae; 72.8 cm).

The second plot (AR2) at Kwakwani had only 491 trees of single recordable stems. *Aspidosperma excelsum* was the largest tree (91 cm) and *Eschweilera pedicellata* had the highest IVI value of 63.671 (138 stems, 28% of the total stems). Two other taxa significant were *Mora gonggrijpii* (Kleinhoonte) Sandw. (Caesal.; IVI=36.486) and *Aspidosperma excelsum* (IVI=15.600). *Inga acrocephala* Steud. (Mimos.), *Mora gonggrijpii*, *Swartzia polyphylla* DC. (Fab.), *Eschweilera pedicellata*, *Chrysophyllum sparciflorum* Klotzsch ex Miq. (Sapotaceae), and *Aspidosperma excelsum* represented the 3% of the total stems over 60 cm DBH. Fifty-six percent of the total stems were under 20 cm.

Lecythidaceae was the most abundant family at Kwakwani, with 254 stems documented for the two plots. Leguminosae was the second most abundant with 184 stems (107 of these were Caesalpinioids in site 2). Next in rank were the Annonaceae with 55 stems over all quadrats in AR1 and Boraginaceae (34 stems). In site 2 these families represented only 19 and 2 stems. Apocynaceae had more stems (26) in AR2 and ranked third in abundance across the plot. All other families had less stems.

Barro Colorado Island, Panama.—In the two 1 ha plots selected from the Barro Colorado Island (BCI) 50 ha plot, the total basal area of trees ≥ 10 cm was 57.153 m²/ha. Information provided for this study includes only data for the main stem on each plot. No data were available for multiple stems and thus these were excluded from this study. The first plot (designated as Hec21 at BCI) had 418 trees. The tree that had the largest diameter on the site was *Hura crepitans* L. (Euphorbiaceae; 102.1 cm DBH). Seventy-five percent of the trees had < 20 cm DBH. Two percent of trees had a DBH > 60 cm: *Brosimum alicastrum* Sw. (Moraceae; 88.5 cm); *Chrysophyllum cainito* L. (Sapotaceae; 88.5), *Jacaranda copaia* (Aubl.) D. Don (82 cm) and *Tabebuia guayacan* (Seem.) Hemsl. (Bignoniaceae; 82 cm); *Prioria copaifera*, (Caesal.; 82 cm); and *Luehea seemannii* Triana & Planch. (Tiliaceae; 76.8 cm). The dominant species for Hec21 were *Faramea occidentalis* (L.) A. Rich. (Rubiaceae; IVI = 18.644), *Trichilia tuberculata* (Triana & Planch.) C.DC. (Meliaceae; IVI = 23.870),

Prioria copaifera, (Caesal.; IVI = 17.581), and *Alseis blackiana* Hemsl. (Rubiaceae; IVI = 10.344). These taxa accounted for 139 trees or one-third of the entire tree census.

The second plot (designated as Hec37 at BCI) contained 447 recordable trees, 62.6% of which were ≤ 20 cm DBH. *Ceiba pentandra* (L.) Gaertn. (Bombacaceae) was the largest tree in the plot with a diameter of 209.5 cm DBH. Other species over 60 cm DBH were *Ficus costaricana* (Liebm.) Miq. (Moraceae; 138 cm), *Tachigali versicolor* Standl. & L.O. Williams (Caesal.; 109.1 cm), *Hura crepitans* (Euphorbiaceae; 99.4 cm), *Aspidosperma cruenta* Woodson (Apocynaceae; 89.0 cm), *Dendropanax arboreus* (L.) Decne. & Planch. (Araliaceae; 83.0 cm), *Brosimum alicastrum* Sw. (Moraceae; 75.3 cm), and *Cecropia insignis* Liebm. (Cecropiaceae; 66.0 cm); *Guapira standleyana* Woodson (Nyctaginaceae; 75.3 cm); *Quararibea asterolepis* Pittier (Bombacaceae; 69.8 cm); and *Guatteria dumetorum* R.E. Fr. (Annonaceae; 63.5 cm). The dominant species on the site were *Faramea occidentalis* (IVI = 23.340) and *Trichilia tuberculata* (IVI=27.239); together, these two accounted for almost 31% of the total countable stems. Other species with high IVI values were two Bombacaceae: *Quararibea asterolepis* (IVI=14.721) and *Ceiba pentandra* (IVI=12.455).

From the two plots examined at Barro Colorado Island, Rubiaceae ranked the highest for individual stems (217). Meliaceae, with 122 trees, ranked second in the "tree per family" category. The Leguminosae contained only 67 stems, 47 of which were Caesalpinioids.

A comparative summary of the most abundant tree species from the six study sites can be found in Table 1.

Statistical analyses.—Non-metric multidimensional scaling (NMS) was used to reduce the datasets at each of the three study sites. In each plot there were several species that exhibited a strong relationship with the ordination scores. These species were displayed on the ordination as a joint plot. The radiating lines of the joint plot reflect the direction and strength of that species that is influencing the separation of the quadrats in the plot. Plot KF1 at Kaieteur had 103 species in the analyses. The final stress was 15.68692 for the 3-D solution with 99 iterations. The Monte Carlo test for this solution was $p \leq 0.0196$. The first two axes accounted for 56.8% of the variance; the first three accounted for 74.1%. Three patterns are seen in the grouping of quadrats based on species assemblages (Fig. 3A). *Dicymbe* spp., *Chamaecrista adiantifolia* var. *pteridophylla*, *Pachira flaviflora* (Pulle) Fern. Alnso. (Bombacaceae) form one group, and *Chamaecrista apoucouita* (Aubl.) H.S. Irwin & Barneby (Caesal.) and *Pterocarpus rohrii* Vahl (Fab.) form a second group; these two groups have a stronger influence in some of the quadrats whereas a third group composed of *Hevea guianensis* Aubl. (Euphorbiaceae), *Inga gracilifolia* Ducke (Mimos.) and species in Meliaceae have a stronger influence on others.

Kaieteur plot KF2 had the fewest species (71) in the dataset. The best result for the dataset is the 3-D ordination from NMS with a stress value of 13.30984 with 162 iterations (Monte Carlo $p \leq 0.0196$). The variance for the first two axes accounted for 66.4% of the variance; if the third axis is included, 82.5% of the variance is accounted for. Quadrats in the plot are separated into species assemblages influenced by two groups: the *Licania alba* (Bernoulli) Cuatrec. (Chrysobalanaceae), Bombacaceae spp., *Clathrotropis macrocarpa* Ducke (Fab.), *Eschweilara* spp., *Ocotea* spp., and *Macrolobium suaveolens* Spruce ex Benth. (Caesal.) group; and the *Henrettea ramiflora* (Sw.) DC. (Melastomataceae), *Sextonia rubra* (Mez) van der Werff (Lauraceae), *Inga* sp.3, and *Catostemma commune* Sandw. (Bombacaceae) in the other (Fig. 3B).

Combining the data from the two plots at Kaieteur, the best result from multiple NMS runs was a 3-D solution (stress = 18.09208, $p \leq 0.0195$) with a variance for the first two axes accounting for 54.6% or 75.0% including the third. The first two axes were chosen for the ordination to best represent the data (Fig. 3C). Axis 1 represents the area of collection and showed little separation between the locations of the plots. Axis 2 represents a clear separation between the species and their assemblages at plots KF1 and KF2. Species that contributed to the discrimination in KF1 were *Dicymbe pharangophila*, *Eperua rubiginosa* Miq. (Caesal.), and *Catostemma fragrans* Benth. (Bombacaceae). Species contributing to discrimination in KF2 were *Eperua* spp., *Sextonia rubra*, *Henriettea ramiflora*, and *Ocotea* spp. There was no overlap in species composition between quadrats of these two plots.

TABLE 1. A comparative summary of the most abundant tree species from Kaieteur National Park and Kwakwani, Guyana, and Barro Colorado Island, Panama. BA = Basal Area; IVI = Importance Value Index. Taxa are sorted from highest to lowest IVI.

Family	Taxa	Total stems	Ave. trees/ (m)	BA (M) DBH	Relative density	Relative domin.	Relative freq.	I V I
Kaieteur plot KF1								
Caesalpiniodeae	*Chamaecrista adiantifolia* (Spruce ex Benth.) H.S. Irwin & Barneby var. *pteridophylla* (Sandwith) H.S. Irwin & Barneby	59/61	0.201	2.306	8.613	7.186	4.253	20.052
Caesalpiniodeae	*Eperua falcata* Aubl.	40/40	0.221	1.788	5.839	5.571	4.017	15.427
Caesalpiniodeae	*Dicymbe pharangophila* R.S. Cowan	20/52	0.237	2.864	2.920	8.924	2.835	14.679
Sapotaceae	*Pouteria* cf. *cuspidata* (A. DC.) Baehni	20/24	0.249	1.580	2.920	4.923	2.599	10.442
Fabiodeae	*Ormosia coutinnoi* Ducke	23/23	0.246	1.333	3.358	4.153	2.599	10.109
Caesalpiniodeae	*Dicymbe* sp.	29/42	0.162	0.950	4.233	2.958	2.835	10.027
Caesalpiniodeae	*Eperua* sp.	22/24	0.221	1.175	3.212	3.661	3.071	9.944
Caesalpiniodeae	*Eperua rubiginosa* Miq.	21/21	0.191	0.770	3.066	2.398	3.308	8.771
Bombacaceae	*Pachira flaviflora* (Pulle) Fern. Alonso)	29/30	0.149	0.600	4.233	1.870	2.363	8.466
Fabiodeae	*Clathrotropis macrocarpa* Ducke	20/20	0.185	0.623	2.920	1.942	2.835	7.697
Leguminosae	Leguminosae sp.	15/18	0.230	0.932	2.190	2.903	2.363	7.455
Euphorbiaceae	*Hevea guianensis* Aubl.	18/20	0.207	0.938	2.628	2.922	1.654	7.204
Fabiodeae	*Pterocarpus* cf. *rohrii* Vahl	16/16	0.200	0.626	2.336	1.950	2.126	6.412
Fabiodeae	*Swartzia schomburgkii* Benth.	11/11	0.233	0.710	1.606	2.211	2.126	5.944
Caesalpiniodeae	*Chamaecrista apoucouita* (Aubl.) H.S. Irwin & Barneby	15/20	0.155	0.420	2.190	1.310	2.363	5.862
Bombacaceae	*Catostemma* cf. *fragrans* Benth.	17/17	0.157	0.355	2.482	1.106	2.216	5.714
Caesalpiniodeae	*Eperua grandiflora* (Aubl.) Benth.	13/13	0.228	0.667	1.898	2.079	1.181	5.158
Meliaceae	Meliaceae sp. 1	8/8	0.312	0.845	1.168	2.632	1.181	4.981
Mimosoideae	*Elizabetha* sp.	5/5	0.447	0.990	0.730	3.085	0.709	4.524
Lecythidaceae	*Eschweilera* ssp.	9/10	0.205	0.444	1.314	1.383	1.654	4.351
Bombacaceae	*Catostemma commune* Sandwith	11/11	0.162	0.251	1.606	0.781	1.890	4.277
Kaieteur plot KF2								
Caesalpiniodeae	*Eperua falcata* Aubl.	54/60	0.209	3.318	6.013	9.687	4.348	20.048
Caesalpiniodeae	*Chamaecrista adiantifolia* (Spruce ex Benth.) H.S. Irwin & Barneby var. *pteridophylla* (Sandwith) H.S. Irwin & Barneby	51/58	0.226	3.091	5.679	9.024	4.783	19.486
Lauraceae	*Ocotea* spp.	74/75	0.166	1.791	8.240	5.231	4.783	18.253
Fabiodeae	*Swartzia schomburgkii* Benth.	50/53	0.219	2.714	5.568	7.924	3.913	17.404
Caesalpiniodeae	*Eperua* sp.	54/59	0.169	1.680	6.013	4.907	4.783	15.702
Bombacaceae	*Catostemma commune* Sandwith	54/57	0.193	2.064	6.013	6.026	3.043	15.082
Fabiodeae	*Ormosia coutinnoi* Ducke	28/28	0.267	1.889	3.118	5.515	3.696	12.328
Caesalpiniodeae	*Chamaecrista apoucouita* (Aubl.) H.S. Irwin & Barneby	35/37	0.151	0.727	3.897	2.122	3.913	9.932

T ABLE 1. continued

Family	Taxa	Total stems	Ave. trees/ (m)	BA (M) DBH	Relative density	Relative domin.	Relative freq.	I V I
Clusiaceae	Clusiaceae sp.	43/43	0.142	0.716	4.788	2.091	3.043	9.922
Melastomataceae	*Henriettea ramiflora* (Sw.) DC.	37/40	0.167	0.942	4.120	2.750	3.043	9.914
Fabiodeae	*Swartzia leiocalycina* Benth.	28/28	0.168	0.739	3.118	2.157	3.696	8.971
Caesalpiniodeae	*Clathrotropis macrocarpa* Ducke	29/30	0.171	0.856	3.229	2.501	3.043	8.773
Anacardiaceae	*Tapirira* sp.	15/15	0.273	1.475	1.670	4.308	2.391	8.369
Lauraceae	Ocotea rubra *Mez*	27/29	0.163	0.649	3.006	1.895	3.261	8.162
Caesalpiniodeae	*Macrolobium suaveolens* Spruce ex Benth.	21/26	0.206	0.999	2.338	2.917	1.957	7.212
Lecythidaceae	*Eschweilera* ssp.	22/25	0.163	0.548	2.450	1.599	3.043	7.092
Annonaceae	*Guatteria* sp.	18/18	0.161	0.412	2.004	1.203	2.826	6.033
Apocynaceae	*Aspidosperma excelsa* Benth.	17/18	0.139	0.287	1.893	0.838	1.957	4.687
Kwakwani plot AR1								
Lecythidacaeae	*Eschweilera pedicellata* (Rich.) S.A. Mori	114/115	23.9	7.400	22.619	31.068	2.131	55.818
Annonaceae	*Unonopsis rufescens* (Baill.) R.E. Fr.	29/29	21.6	1.249	5.754	5.244	0.888	11.886
Apocynaceae	*Aspidosperma excelsum* Benth.	26/26	25.3	1.363	5.159	5.722	0.977	11.858
Annonaceae	*Bocageopsis multiflora* (Mart.) R.E. Fr.	21/21	23.7	1.361	4.167	5.714	0.977	10.858
Boraginaceae	*Cordia sagotii* I.M. Johnst.	33/33	15.9	0.677	6.548	2.842	0.888	10.278
Fabiodeae	*Swartzia schomburgkii* Benth.	24/24	22.2	1.186	4.762	4.979	0.089	9.830
Rosaceae	*Prunus* sp.	30/30	15	0.566	5.952	2.376	1.421	9.749
Moraceae	*Pourouma cucura* Standl. & Cuatrec.	13/13	24.1	0.763	2.579	3.203	0.888	6.662
Anacardiaceae	*Tapirira guianensis* Aubl.	15/15	20.4	0.604	2.976	2.536	0.888	6.400
Celastraceae	*Goupia glabra* Aubl.	13/14	21.6	0.517	2.579	2.171	0.444	5.194
Fabiodeae	*Clathrotropis brachypetala* (Tul.) Kleinhoonte	14/14	14.2	0.242	2.778	1.016	0.888	4.682
Kwakwani plot AR2								
Lecythidaceae	*Eschweilera pedicellata* (Rich.) S.A. Mori	138/138	26.8	9.289	28.106	33.045	2.520	63.671
Caesalpiniodeae	*Mora gonggrijpii* (Kleinhoonte) Sandwith	80/80	23.3	5.166	16.293	18.378	1.815	36.486
Apocynaceae	*Aspidosperma excelsum* Benth.	26/26	26.7	2.500	5.295	8.894	1.411	15.600
Chrysobalanaceae	*Couepia guianensis* Aubl.	14/14	33.3	1.535	2.851	5.461	1.008	9.320
Sapotaceae	*Chrysophyllum sparsiflorum* Klotzsch ex Miq.	12/12	28.3	1.039	2.444	3.696	0.807	6.947
Fabiodeae	*Swartzia schomburgkii* Benth.	18/18	19	0.644	3.666	2.291	0.907	6.864
Lauraceae	*Chlorocardium rodiaei* (R.H. Schomb.) Rohwer, H.G. Richt. & van der Werff	15/15	22.3	0.647	3.055	2.302	1.008	6.365
Fabiodeae	*Swartzia polyphylla* DC.	8/8	33.8	1.023	1.629	3.639	0.807	6.075
Violaceae	*Paypayrola longifolia* Tul.	19/19	11.6	0.209	3.870	0.744	1.311	5.925
Myristicaceae	*Iryanthera juruensis* Warb.	17/17	13.2	0.246	3.462	0.875	1.109	5.446
Rosaceae	*Prunus* sp.	11/11	18.7	0.345	2.240	1.227	0.706	4.173

Table 1. continued

Family	Taxa	Total stems	Ave. trees/ (m)	BA (M) DBH	Relative density	Relative domin.	Relative freq.	I V I
Barro Colorado Island: Hec21*								
Meliaceae	*Trichilia tuberculata* (Triana & Planch.) C.DC.	42	26.5	2.742	10.048	12.319	1.503	23.870
Rubiaceae	*Faramea occidentalis* (L.) A.Rich.	58	12.0	0.671	13.876	3.015	1.753	18.644
Caesalpiniodeae	*Prioria copaifera* Griseb.	17	34.6	2.785	4.067	12.512	1.002	17.581
Rubiaceae	*Alseis blackiana* Hemsl.	22	20.6	0.908	5.263	4.079	1.002	10.344
Moraceae	*Brosimum alicastrum* Sw.	8	38.1	1.415	1.914	6.357	0.501	8.772
Arecaceae	*Oenocarpus mapora* H. Karst.	24	11.1	0.230	5.742	1.033	1.169	7.944
Bombacaceae	*Quararibea asterolepis* Pittier	11	27.8	0.856	2.632	3.846	0.918	7.396
Bignoniaceae	*Jacaranda copaia* D. Don.	6	43.7	1.177	1.435	5.290	0.417	7.142
Burseraceae	*Tetragastris panamensis* Kuntze	9	25.3	0.880	2.153	3.953	0.584	6.690
Apocynaceae	*Tabernaemontana arborea* Rose	10	26.7	0.701	2.392	3.149	0.668	6.209
Lecythidaceae	*Gustavia superba* O. Berg	9	27.1	0.549	2.153	2.466	0.751	5.370
Euphorbiaceae	*Hura crepitans* L.	2	61.1	0.850	0.479	3.819	0.167	4.465
Tiliaceae	*Apeiba aspera* Aubl.	7	26.4	0.506	1.675	2.273	0.417	4.365
Rubiaceae	*Randia armata* DC.	11	12.7	0.146	2.632	0.656	0.835	4.123
Barro Colorado Island: Hec37*								
Meliaceae	*Trichilia tuberculata* C. DC.	59	25.2	3.748	12.369	13.209	1.661	27.239
Rubiaceae	*Faramea occidentalis* (L.) A. Rich.	80	12.3	0.979	17.897	3.450	1.993	23.340
Rubiaceae	*Alseis blackiana* Hemsl.	25	29.5	2.108	5.593	9.422	1.329	16.344
Bombacaceae	*Quararibea asterolepis* Pittier	20	36.3	2.601	4.474	9.167	1.080	14.721
Bombacaceae	*Ceiba pentandra* (L.) Gaertn.	1	209.5	3.447	0.224	12.148	0.083	12.455
Olacaceae	*Heisteria concinna* Standl.	15	17.9	0.415	3.356	1.463	0.831	5.650
Moraceae	*Ficus costaricana* Miq.	1	138.0	1.496	0.224	5.272	0.083	5.579
Myristicaceae	*Virola sebifera* Aubl.	11	23.1	0.519	2.461	1.829	0.831	5.121
Meliaceae	*Guarea guidonia* (L.) Sleumer	12	19.8	0.422	2.685	1.487	0.831	5.003
Lecythidaceae	*Gustavia superba* O. Berg	11	21.0	0.403	2.461	1.420	0.748	4.629
Moraceae	*Brosimum alicastrum* Sw.	8	23.5	6.629	1.790	2.217	0.581	4.588
Nyctaginaceae	*Guapira standleyana* Woodson	5	41.3	0.803	1.119	2.830	0.415	4.364
Euphorbiaceae	*Drypetes standleyi* G.L. Webster	12	15.4	0.240	2.685	0.846	0.831	4.362
Cecropiaceae	*Cecropia insignis* Liebm.	6	36.1	0.730	1.342	2.573	0.415	4.330
Fabiodeae	*Swartzia simplex* Spreng. var. *grandiflora* (Raddi) R.S. Cowan	10	21.7	0.394	2.237	1.389	0.581	4.207
Burseraceae	*Protium tenuifolium* Engl.	10	19.3	0.328	2.237	1.156	0.664	4.057

*** Total stems not provided for Barro Colorado Island**

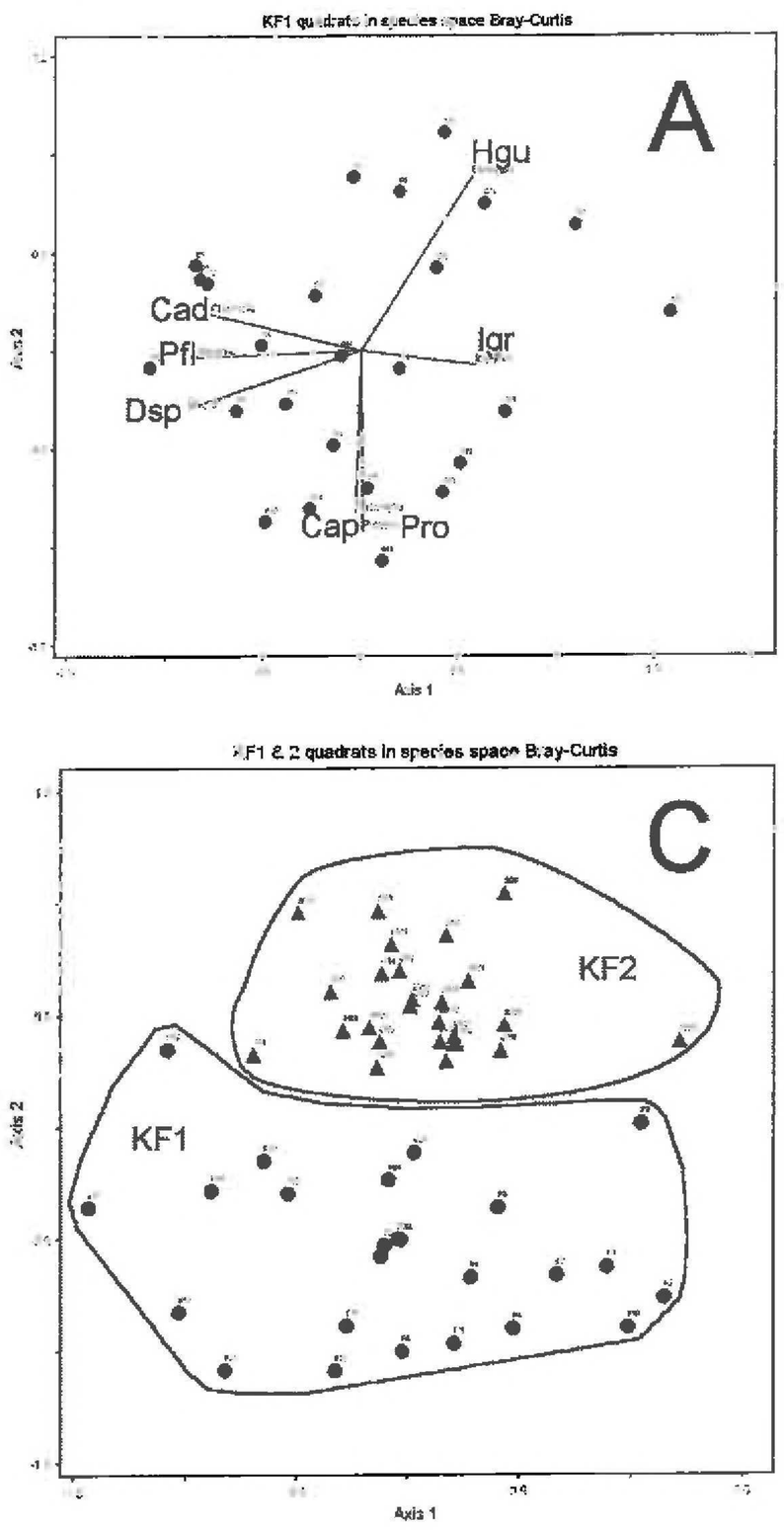


Fig. 3. Non-metric multidimensional scaling (NMS) ordination analyses of (A) Kaieteur, KF1, resulted in some degree of separation between three groups based on species assemblages dominated by: *Dicymbe* spp. [Dsp], *Chamaecrista adiantifolia* var. *pteridophylla* [Cad], *Pachira flaviflora* [Pfl] in one group, *Chamaecrista apoucouita* [Cap] and *Pterocarpus rohrii* [Pro] in the second and *Hevea guianensis* [Hgu] and *Inga gracilifolia* [Igr] in the third; (B) the quadrats of Kaieteur, KF2, separate into two groups with species assemblages of *Licania alba* [Lal], Bombacaceae spp. [Bsp], *Clathrotropis macrocarpa* [Cma], *Eschweilara* ssp. [Esp], *Ocotea* spp. [Osp], and *Macrolobium suaveolens* [Msu] in one group and *Henrettea ramiflora* [Hra], *Sextonia rubra* [Sru], *Inga* sp.3 [Is3], and *Catostemma commune* [Cco] in the other group; (C) combined species data from both plots [KF1 & KF2] at Kaieteur indicate little to no overlap in species assemblages between the quadrats; (D) ordination of tree species at Kwakwani, AR1, with quadrats separating into three groups based on analyses; these groups were dominated by: *Unonopsis rufescens* [Uru], *Cordia sagotii* [Csa], *Tapirira* sp.2 [Ts2] in one group, *Miconia hypoleuca* [Mhy], *Bocageopsis multiflora* [Bmu] in the second, and *Eschweilera pedicellata* [Epe] as the only species in the third; (E) at the second plot at Kwakwani, AR2, *Eschweilera pedicellata* and *Mora gonggrijpii* significantly outweighed the other species and were removed from the calculations. The subdominant species that influenced the groupings were *Miconia hypoleuca* [Mhy], *Inga pezizifera* [Ipe], *Prunus* sp. [Psp], *Chlorocardium rodiaei* [Cro], *Margaritaria nobilis* [Mno] and *Ocotea* spp. [Osp]; (F) the combined species data from both plots [AR1 & AR2] at Kwakwani had an overlap of approx. 50% of the quadrats between the study sites.

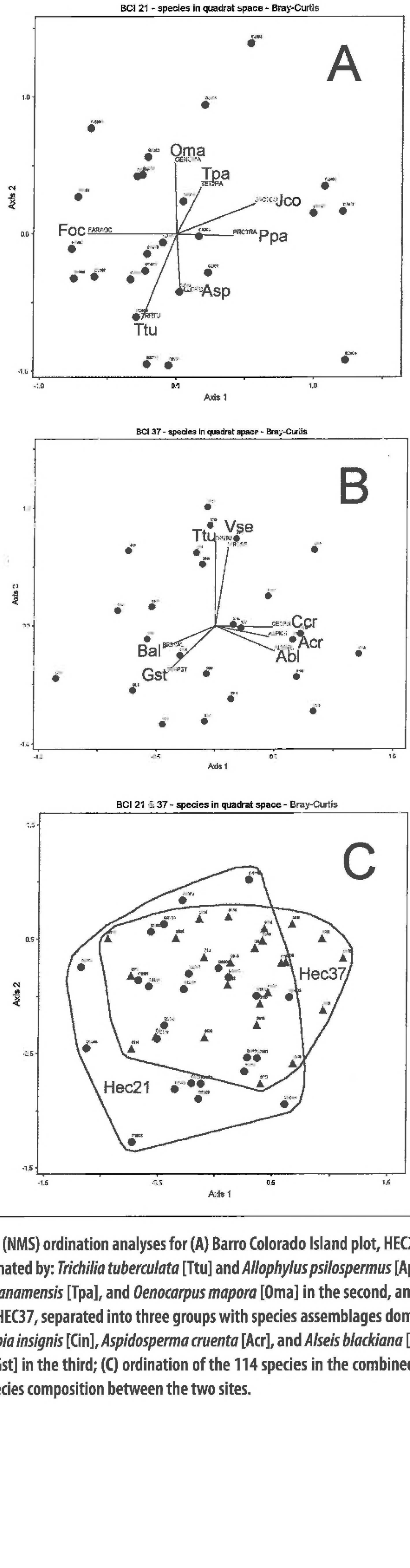


Fig. 4. Non-metric multidimensional scaling (NMS) ordination analyses for (A) Barro Colorado Island plot, HEC21, resulted in separation between three groups based on species assemblages dominated by: *Trichilia tuberculata* [Ttu] and *Allophylus psilospermus* [Aps] in the first group, *Protium panamense* [Ppa], *Jacaranda copaia* [Jco], *Tetragastris panamensis* [Tpa], and *Oenocarpus mapora* [Oma] in the second, and *Faramea occidentalis* [Foc] in the third; (B) the quaddrats of Barro Colorado Island HEC37, separated into three groups with species assemblages dominated by: *Trichilia tuberculata* [Ttu] and *Virola sebifera* [Vse] in the first group, *Cecropia insignis* [Cin], *Aspidosperma cruenta* [Acr], and *Alseis blackiana* [Abl] in the second, and finally, *Brosimum alicastrum* [Bal] and *Guapira standleyana* [Gst] in the third; (C) ordination of the 114 species in the combined dataset for Barro Colorado Island plots [Hec21 7 Hec37] indicates a similarity of species composition between the two sites.

Ordination was used to reduce the datasets at the Kwakwani study site. Site AR1 had 84 species with a final analysis in a 3-D solution of 15.71292 (stress) over 82 iterations ($p \leq 0.0196$). The overall patterns between the quadrats indicate some differences in species composition between the plots. The quadrats separated into several groups (Fig. 3D). These assemblages were defined by *Unonopsis rufescens* (Baill.) R.E. Fr. (Annonaceae), *Cordia sagotii* I.M. Johnst. (Boraginaceae), *Eschweilera pedicellata*, *Miconia hypoleuca* (Benth.) Triana (Melastomataceae), *Bocageopsis multiflora* (Mart.) R.E. Fr. (Annonaceae) and *Tapirira* sp.2 (Anacardiaceae). The first two axes accounted for 53.0% of the variance. Including the third, 72.9%of the variance was accounted for.

At site AR2, there were 58 species in the matrix. *Eschweilera pedicellata* and *Mora gonggrijpii* were abundant throughout the plot. Since their higher weight contributed more than the other species, NMS failed to find a useful ordination. *Eschweilera pedicellata* and *Mora gonggrijpii* were deleted for remaining calculations. The result was a 4-D solution (stress = 13.80266; $p \leq 0.0392$) for this plot (Fig. 3E). The first two axes accounted for 18.7%, and the third added only 34.6% of the variance. These assemblages were defined by the following species in the plot: *Miconia hypoleuca* (Benth.) Triana (Melastomataceae), *Inga pezizifera* Benth. (Mimos.), *Prunus* sp. (Rosaceae), *Chlorocardium rodiei* (R.H. Schomb.) Rohwer, H.G. Richt. & van der Werff (Lauraceae), *Ocotea* spp., and *Margaritaria nobilis* L.f. (Euphorbiaceae). Combining the datasets for both plots at Kwakwani resulted in 93 species in the analysis. NMS ordination yielded a 3-D solution with a stress of 19.64717 ($p \leq 0.0196$) over 326 iterations. The first two axes accounted for 44.1% of the variance (65.7% with all three). Fifty percent of the quadrats from both plots had species compositions that were similar. *Swartzia schombergkii*, *Prunus* sp., *Mora gonggrijpii*, *Couepia guianensis* Aubl. (Chrysobalanaceae), and *Aspidosperma excelsum* were the species that define the assemblages in the BCI plots. *Eschweilera pedicelliata* was abundant in both plots (Fig. 3F).

At the Barro Colorado Island (BCI) Hec21 plot, a total of 92 species was observed. The final stress for the 3-D solution was 15.82730 ($p \leq 0.0196$) in 88 iterations. The first two axes accounted for 49.2% of the variance (73.8% with all three). Figure 4A shows the result of the non-metric scaling. The angle and length of the radiating lines in the joint plot indicate the direction and strength that each species has with the ordination score. Radiating vectors indicated that *Trichilia tuberculata*, *Allophylus psilospermus* Radlk. (Sapindaceae), *Protium panamense* (Rose) I.M. Johnst. (Burseraceae), *Faramea occidentalis*, *Jacaranda copaia*, *Tetragastris panamensis* Kuntze (Burseraceae), and *Oenocarpus mapora* Karst. (Arecaceae) had the strongest relationship with the ordination scores.

The BCI plot Hec37 had 82 species; the ordination had a final stress of 17.47696 over 131 iterations ($p \leq 0.0392$). The first two axes accounted for 30.5% of the variance and the first three, 61.1% of variance. The species that contributed to discrimination in this plot were *Trichilia tuberculata*, *Virola sebifera* Aubl. (Myristicaceae), *Cecropia insignis*, *Aspidosperma cruenta*, *Alseis blackiana*, *Brosimum alicastrum*, and *Guapira standleyana* (Fig. 4B).

A total of 114 species in the two BCI plots was observed. The resulting ordination of the combined plots produced a 3-dimensional solution with a stress of 21.77097 ($p \leq 0.0392$) in 400 iterations. The variance explained by the first two axes was 33.6% and 58.1% including the third. The quadrats of the two plots overlapped significantly, indicating a similarity of species composition within each plot (Fig. 4C). The species with the strongest relationship in this ordination were *Trichilia tuberculata*, *Adelia triloba* Hemsl. (Euphorbiaceae), *Oenocarpus mapora* and *Jacaranda copaia*.

DISCUSSION

Establishing two permanent biodiversity monitoring plots at Kaieteur National Park has provided Guyana with the scientific data required for the prioritization of conservation initiatives. This study provides baseline data on tropical woody plant communities to aid in measuring ecological change over time and to help distinguish between natural and human impact. Measuring relative density, relative frequency, relative dominance, and importance index values of individual species provides information on how species

are distributed within the forest and how they contribute to the community in which they live. Using a standardized methodology for surveying all trees ≥ 10 cm DBH ensures comparability with other study sites and provides a framework for studying the dynamics of tropical forests. This survey at Kaieteur resulted in 133 taxa representing 1586 trees (1,725 stems ≥ 10 cm in DBH) almost twice the number of trees from the Kwakwani, Guyana or Barro Colorado Island, Panama. The density of trees at Kaieteur were similar to a caatinga forest on white sand at Pico da Neblina in Brazil where 1569 trees were measured in two one-hectare plots (Boubli 2002). The number of stems recorded in each plot at Kaieteur bordered on the upper range of stems per hectare (965 stems ha^{-1}) found on similar plot studies. This high number of stems were found by Davis and Richards (1933, 1934) in five plots at Moraballi Creek, Guyana (460 to 919 trees per 122 x 122 m plot) where as those of similar studies in the Neotropics for trees ≥ 10 cm DBH have not been. Sabatier and Prévost (1990), Poncy et al. (1998), and Bordenave et al. (1998) found densities of 473 to 570 stems per hectare at Les Nouragues, French Guiana, and up to 882 stems per hectare in one particular transect (Sabatier & Prévost 1990). Johnston and Gillman (1995) recorded 357 to 742 trees per hectare at the four one-hectare study plots at Kurupukari, Guyana. At the El Caura Forest Reserve, South Venezuela, mean densities ranged from 563–573 trees ha^{-1} (Castellanos 1998). In Manaus, Brazil mean densities were 550 stems ha^{-1} (Ferreira & Rankin-de-Mérona 1998).

Davis and Richards (1934) noted that the forest at Moraballi Creek dominated by *Eperua falcata* had an extraordinary large number of trees ha^{-1} and that Leguminosae was the most abundant family (Whitton 1962). This was also noted by Boubli (2002) at Neblina where *Eperua leucantha* Benth. accounted for a large percentage of the stems. Guyana's rain forests can be dominated by one to several species, these often in the same family (Davis & Richards 1933; Fanshawe 1952; Whitton 1962; Henkel 2003). Kwakwani's plots were dominated by Lecythidaceae (30.9%) and Kaieteur's (47%) were dominated by Leguminosae. This is not unique to Guyana as a Lecythidaceae or Leguminosae dominance can be found in many other tropical forests, e.g., Richards 1952; Whitton 1962; ter Steege 1993; Nascimento & Proctor 1994; Henkel 2003.

Stem diameters were summarized into two categories (10 cm increments and percentage of stems per class size) in order to facilitate comparisons between the study sites (Table 2). The distribution of tree per class size in the six plots shows a characteristic inverse J-shape (Fig. 5) typical of forests that have been relatively undisturbed in the recent past (Lindeman & Mori 1989), with over 56% of the trees equal to or less than 20 cm DBH. Overall, the stem class size distributions from 20.1 cm to 60 cm DBH at Kaieteur were comparatively similar to Kwakwani and BCI in this paper. Total percentage of stems below the 40.1 cm DBH class in each of the three study sites ranged from a low of 86.7% at BCI to 95.9% at Kaieteur plot KF2. Boubli (2002) commented that 46% of trees at Neblina were small in girth while Whitton (1962) commented that in the Wallaba forests of Guyana, very few trees exceed 70 cm in diameter. At Kaieteur only ca. 2% reached the larger diameters with only three species, these all Caesalpinioid legumes, reaching over 30 cm DBH: *Eperua falcata, Chamaecrista adiantifolia* var. *pteridophylla* and *Swartzia schomburgkii*.

The total calculated basal area/ha from the three sites in this study ranged from 52 to 66 m^2 / ha. Kwakwani and BCI were similar to the 53 m^2/ha found by Whitton (1962) and Mori and Boom (1987) at Saül, French Guiana, but higher than those found in the forest plots (27–34 m^2/ha) of Central Amazonia (Rankin-de-Merona et al. 1992). Kaieteur's total basal area (66 m^2/ha) was similar to that of Neblina (Boubli 2002, 73 m^2/ha).

In order to understand the importance value index (IVI) of each species and how it contributes to the community one has to look at its relative parameters. Of all the Caesalpiniodeae legumes at Kaieteur two species, *Eperua falcata* and *Chamaecrista adiantifolia* var. *pteridophylla*, yielded a total IVI value of 75.0. These species were widely spread throughout the plots, had a more stems than other species. In the lowland area of Kwakwani, the highest IVI values (119.5) for both sites came from one species of Lecythidaceae, *Eschweilera pedicellata*. This species dominated the plots and was higher than the Lecythidaceae at La Fumée Mountain, French Guiana (Mori & Boom 1987). Such high IVI values have only been recorded elsewhere by Gibbs et al. (1980) for *Cyclolobium vecchii* A. Samp. ex Hoehne (Leguminosae; IVI=82) and *Sebastiania klotschiana*

TABLE 2. Stem class size in cm DBH (number of stems/percent of stems) at Kaieteur National Park and Kwakwani, Guyana, and Barro Colorado Island, Panama.

		≥ 10.0	≥ 20.1	≥ 30.1	≥ 40.1	≥ 50.1	≥ 60.1	
Kaieteur								
	Plot 1	488 / 64.3	147 / 19.4	72 / 9.5	28 / 3.7	15 / 2.0	8 / 1.0	
	Plot 2	673 / 69.6	201 / 20.8	53 / 5.5	19 / 2.0	11 / 1.1	10 / 1.0	
Kwakwani								
	Site 1	316 / 62.2	110 / 21.6	45 / 8.9	14 / 2.8	7 / 1.4	13 / 2.6	
	Site 2	277 / 56.4	107 / 21.7	60 /12.2	20 / 4.1	12 / 2.4	15 / 3.1	
Barro Colorado Island								
	Hec21	287 / 68.7	52 / 12.4	38 / 9.1	19 / 4.6	9 / 2.1	13 / 3.1	
	Hec37	280 / 62.6	88 / 19.7	36 / 8.1	13 / 2.9	14 / 3.1	16 / 3.6	

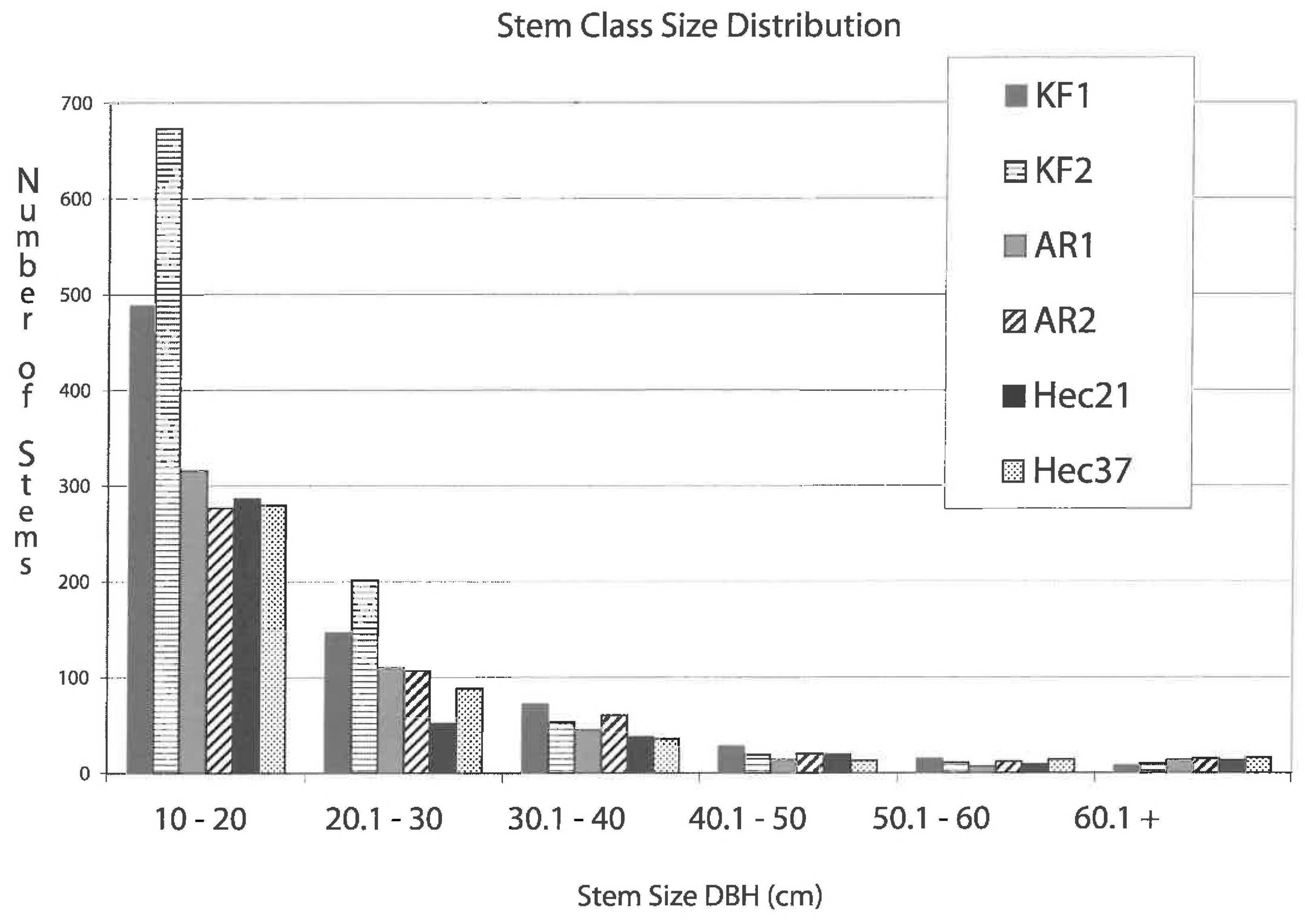


FIG. 5. Distribution of stem diameters in the six study plots of Kaieteur (KF), Kwakwani (AR) and Barro Colorado Island (Hec) shows the characteristic inverse J-shape typical of relatively undisturbed forests.

(Muell. Arg.) Muell. Arg. (Euphorbiaceae; IVI=119) from his survey in Mugi-Guiçu, Brazil. At Barro Colorado Island to species in different families scored high, *Trichilia tuberculata* (Meliaceae, IVI=51.1) and *Faramea occidentalis* (Rubiaceae, IVI=41.9).

When the plot data were examined at the family level, there were 33 families at Kaieteur and 36 at Kwakwani. The number of families in the Guyana plots was lower than the number of families recorded by Balslev et al. (1987) for the floodplain (44) and non-flooded forests (53) of Añangu, Ecuador. It was also lower than the 42 families at BCI. Thirty-three percent of the families were found in all three study sites, with

TABLE 3. Dominant families within the three sites with a combined total of over 50% of the stems: Kaieteur (KF), Kwakwani (AR), and Barro Colorado Island (BCI). Numbers shown are percentages of overall stems per family found at each site.

	KF	AR	BCI
Annonaceae	-	7.4	-
Apocynaceae	-	5.2	-
Arecaceae	-	-	5.6
Bombacaceae	8.2	-	-
Euphorbiaceae	-	-	4.3
Lauraceae	9.5	-	-
Lecythidaceae	-	25.4	-
Leguminosae	49.2	18.4	7.6
Meliaceae	-	-	14.1
Rosaceae	-	4.1	-
Rubiaceae	-	-	25.1

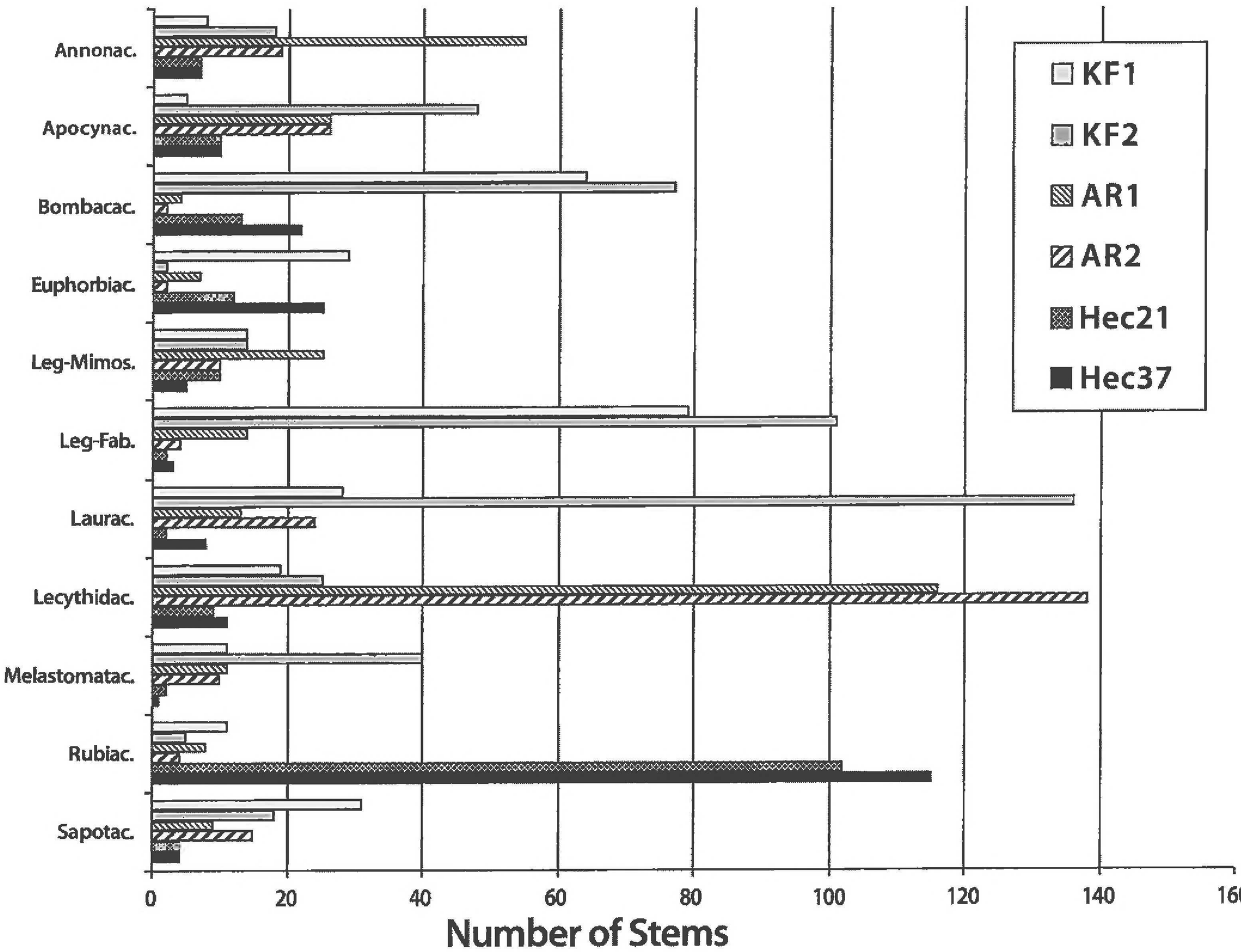


FIG. 6. Total number of stems for each family shared by Kaieteur and Kwakwani, Guyana and Barro Colorado Island, Panama (Caesalpinioideae dominated the plots at Kaieteur with over 300 stems/ha outweighing all other families so it was excluded from this figure.)

the dominant families varying among the sites (Table 3). The total number of stems for each family shared by all three sites is compared in Figure 6. Caesalpinioideae dominated the plots at Kaieteur with over 300 stems/ha. Subsequently, it was necessary to leave this subfamily of Leguminosae out of the comparison so that the bars on the graph representing families with less than 50 stems would be displayed.

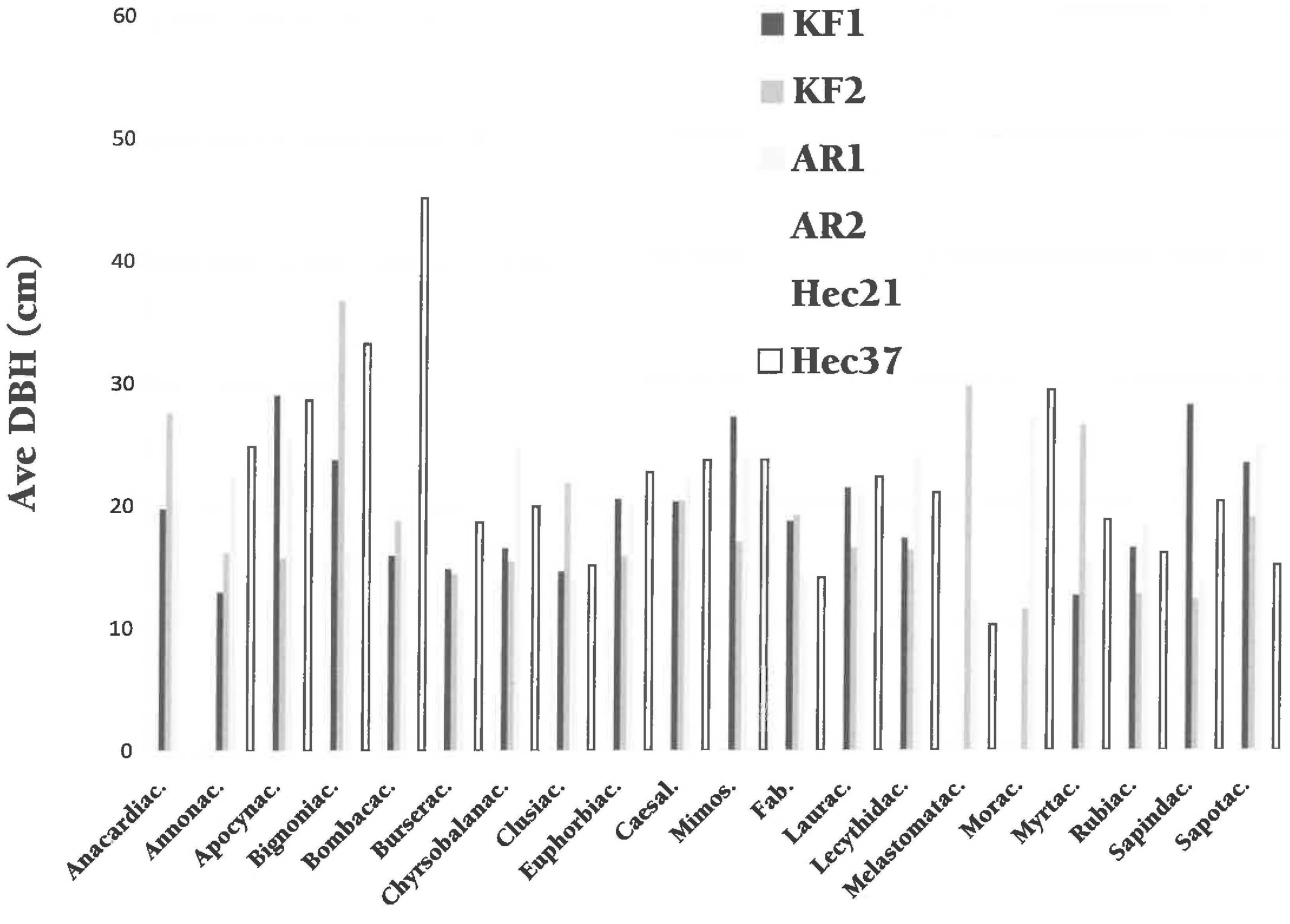


Fig. 7. Average diameter at breast height (DBH) of the major tree families at Kaieteur and Kwakwani, Guyana and Barro Colorado Island, Panama. Key to the abbreviations: KF1=Kaieteur, plot 1; KF2=Kaieteur, plot 2; AR1=Kwakwani, site 1; AR2=Kwakwani, site2; Hec21=Barro Colorado Island, plot 1; Hec37=Barro Colorado Island, plot 2.

When the average diameter at breast height of major tree families at Kaieteur, Kwakwani, and BCI were compared (Fig. 7), the DBH ranged from 10.2 cm (Melastomataceae) to 47.7 cm (Bombacaceae). The largest tree recorded among the research sites was an individual of *Ceiba pentandra*, Bombacaceae, from Hec37 at Barro Colorado Island, with a DBH of 209.5 cm.

From the 325 taxa recorded for the three study sites, only 3% (10 species) of all species were shared between the plots. *Apeiba aspera, Brosimum alicastrum,* and *Virola surinamensis* were shared between Barro Colorado Island and Kwakwani. *Catostemma fragrans, Licania alba, Swartzia schomburgkii,* and *Tapirira guianensis* were shared by Kwakwani and Kaieteur. BCI and Kaieteur shared only *Pterocarpus rohrii*. The only species shared by all three sites was *Jacaranda copaia*. Thus, there is a substantial lack of overlap in species composition among these tropical tree communities. Comparing genera among sites, only 6% were shared among Kaieteur, Kwakwani and Barro Colorado Island. These were *Aspidosperma, Inga, Jacaranda, Licania, Ocotea, Pouteria, Protium,* and *Swartzia*. When pair-wise comparisons were made between the sites, BCI and Kwakwani shared 8.1% of their genera. Kwakwani and Kaieteur Falls shared 6.3% and 5.0% was shared between BCI and Kaieteur. Based on a phytogeographical study of the taxa at Kaieteur, the flora of this area has its strongest affinity (42%) with the Guiana Shield area of South America with only about 15% of the taxa having a widespread distribution across the Neotropics (Kelloff & Funk 2004).

Statistically, non-metric (NMS) ordination on ecological data derived from PC-ORD has helped to describe the vegetation data from the plots at Kaieteur National Park and Kwakwani, Guyana and Barro

Colorado Island, Panama. In all six plots, the first two axes describe the relationship or dissimilarity between the quadrats (in ordinary space) and represent this variation in ordination space (McCune & Grace 2002). The quadrats with floristic similarities tend to form loose clusters. In the joint plots these similarities suggest trends that can be indicators of microhabitats induced by substrate characteristics, hydrology and/or other edaphic effects in the site. The Janzen-Connell model for tropical tree diversity proposes that seeds and seedlings in proximity of conspecific adults are have a higher mortality rate resulting in recruitments some distance from the parent tree leaving space for colonization by other species (Schupp 1992). Other factors to consider are the ability of the species to disperse its seeds, the competition for light or nutrients, pollinators.

Ordination of tree species at Kaieteur separated the 20 × 20 m quadrats in each plot primarily by species composition. The quadrats were strongly correlated with some of the less dominant tree species such as *Eperua rubiginosa, Inga gracilifolia, Bombax flaviflora, Dicymbe* sp., *Hevea guianensis* in KF1 and *Pouteria cuspidata, Clusia* sp., *Tapirira* sp., *Licania canella* and *Byrsonima incarnata* in KF2. Some species such as *Hevea guianensis* that grows along more inundated soils and *Bombax flaviflora* of the dryer soils may help explain the variation in the plots. Although the soils of the Potaro Plateau are largely composed of porous white sand with very little nutrients, slope, accumulation of leaf litter, and hydrology can change over relatively short distances (C. Kelloff, pers. obs.). Although dominated by *Eperua falcata* and *Chamaecrista adiantifolia* var. *pteridophylla*, the two plots at Kaieteur indicate differences in the forest community over very short distances (Fig. 5). This was not the case at Kwakwani or BCI where analyses indicated some overlap in species composition between the quadrats of the plot pairs at each study site.

Although a forest type may be designated based on the dominant species, the forest is not without an array of subdominant or even rare species that have an overall large effect on the floristic composition of the forest. Such changes can occur over distance and time with changes in light (tree falls), seed dispersal, soil composition or by turn-over (David & Richards 1934). An example of one such change is in the Kaburi district of Guyana where the *Eperua falcata* forests were replaced over time by *Dicymbe corymbosa* Spruce ex Benth. which expanded its dominance by self-pollarding, thus replacing mature trees with large clumps of slender stems (Davis & Richards 1934) and eventually crowding out the other species. The forest at Kaieteur could not be considered a monodominant stand nor could it be considered strictly a Wallaba (*Eperua*) forest. As seen in plot 2 *Chamaecrista adiantifolia* var. *pteridophylla* became the dominate species in that area of the forest. The main family that dominated the forest was the Caesalpiniodeae of the Leguminosae with over 300 stems. The subdominant families range from Lauraceae, Bombacaceae, Clusiaceae, and Fabiodeae.

CONCLUSION

Plots can be a powerful tool for providing long-term information on forest composition, diversity and structural change. They can then be used to assess changes in the forest over time, and the information gathered from plots can be used to understand how other physical parameters may influence species composition and distribution (Dallmeier & Comiskey 1998).

The two plots established at Kaieteur National Park were only a small sampling of the riparian forests of the Potaro Plateau. The information gathered on the tree composition of just one area on the plateau demonstrates the diversity and turnover in this forest. The Wallaba (*Eperua*)–mixed forest plot study at Kaieteur had a larger number of trees per unit area over 10 cm DBH and represented almost twice the stems surveyed in the Mora forests at Kwakwani, Guyana or in the lowlands of Barro Colorado Island, Panama. The plots at Kaieteur were similar to the white sand forest studies by Whitton (1962) at Amatuk, Guyana and by Boubli (2002) at Neblina, Brazil, with their large number of trees and dominance of the family Leguminosae. One hypothesis presented by Torti and Coley (1999) suggested that legumes may be more successful in this region because they have ectomycorrhizal fungi that are good scavengers for nutrients in the otherwise nutrient poor soils and that these fungi suppress saprophytic fungi that are potentially detrimental to this symbiosis. A study by ter Steege and Hammond (2001) suggested that seedlings were compensating for low

light conditions by providing an internal energy source in the form of large cotyledons. Bulky endosperms sustained larger seedlings and supported juvenile plants when light were insufficient. Although designated as a Wallaba-mixed forest, Kaieteur did not have a single dominant species such as *Eschweilera pedicellata* that was dominant in the lowland forest of Kwakwani. Studies have shown that Kaieteur has a strong affinity to the Guiana Shield flora (Kelloff & Funk 2004) with an upland element of the Roraima formation. This was noted from this study with via a similarity of Kaieteur to Pico da Neblina in Brazil.

Non-metric multidimensional scaling (NMS) methods for examining vegetation data from ecological communities are valuable tools for researchers. NMS examines the relationship between floristic dissimilarities of vegetation and subsequent ecological inference. Statistical analyses of the plots at Kaieteur National Park revealed dissimilarities in the species composition between the plot pairs. This suggests subtle changes in microhabitats and species dynamics of the subdominant tree taxa on the Potaro Plateau.

This study has shown that two 1 ha plots can adequately demonstrate how diverse tree species are in one section of the forest; furthermore, it indicates that sampling was probably too small to capture all of the different habitats represented at Kaieteur National Park. It still remains to be understood why the Caesalpiniodeae and in particular the *Eperua* and *Chamaecrista* dominated the forest. Does this indicate favorable ecological condition, the Janzen-Connell effects or can the Caesalpiniodeae legumes with its root nodules thrive better is the nutrient poor soil of the Potaro Plateau? To answer these questions more studies need to be done on the soils of the plateau.

Forests on white sand generally have a lower alpha-diversity than those on terra firme (ter Steege et al. 2000a) but noted for their monodominance and high abundance of several tree families, such as the Caesalpiniaceae. These forests also have trees that are locally abundant but globally restricted such as the Greenheart, *Chlorocardium rodiei* (Rob. Schomb.) Rohwer, Richter, & van der Werff (Lauraceae), in central Guyana. Development or poorly designed logging and mining practices can quickly lead to irreversible damages to the forests and habitats, with eventual species loss or extinction. Analysis of the diversity and the composition on the scale of plots can provide some of the best information needed define protected areas in Guyana (ter Steege et al. 2000b; Kelloff 2003). It is on this scale that we can best understand plant spatial distributions and how radically these can change over a relatively small geographic area.

The information collected in the plot study at Kaieteur National Park can be useful for monitoring compositional or structural changes of the forest over time or for impact assessment. This information, along with the "Checklist of the Plant of Kaieteur National Park, Guyana" provides data on the plant taxa found on the Potaro Plateau in the vicinity of Kaieteur National Park. In addition to minimizing habitat damage due to industrial development, these data can be used to provide the framework for conservation efforts in the park as well as for the development of ecotourism.

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